Subterranean Biology 43: 145–168 (2022)
doi: 10.3897/subtbiol.43.85804
https://subtbiol.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

Coframalaxius bletteryi gen. et sp. nov. from subterranean habitat in Southern France (Hemiptera, Fulgoromorpha, Cixiidae, Oecleini)

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Academic editor: Oana Teodora Moldovan | Received 25 April 2022 | Accepted 6 June 2022 | Published 15 July 2022

http://zoobank.org/4D73DEA3-FE14-46A2-A689-FE5CEE4B760E

Citation: Le Cesne M, Bourgoin T, Hoch H, Luo Y, Zhang Y (2022) *Coframalaxius bletteryi* gen. et sp. nov. from subterranean habitat in Southern France (Hemiptera, Fulgoromorpha, Cixiidae, Oecleini). Subterranean Biology 43: 145–168. https://doi.org/10.3897/subtbiol.43.85804

Abstract

A new planthoppers genus and species of Cixiidae Oecleini, *Coframalaxius bletteryi* **gen. et sp. nov.** newly discovered in a cave near Nice in southern France, is described. Molecular analysis confirms the morphology-based classification of *Coframalaxius* as sister to *Trigonocranus* within the Oecleni. Several morphological characters are further discussed. A double-grasping coxo-femoral and femoro-tibial system is regarded as apomorphic for the oecline taxa and would allow the nymph to firmly grab the roots and rootlets on which it feeds or use to progress in the soil. Wing vein patterns are discussed in the Cixiidae: 1) for the forewings, Oecleini belong to the trifid type of the anterior MP branch, leading to the reinterpretation of some recently described Neotropical species, 2) for the hindwing, four connection types (U-, V-, Y- and I-types) between MP and CuA are described. Oecleini belongs to I-type with a complete fusion of MP_{3+4} with CuA_1. Although the area where the cave is located is well-studied with respect to its regularly sampled epigean fauna for many years, the taxon is new to science, highlighting its probable completely hypogean life cycle and leading to consider *Coframalaxius bletteryi* as an eutroglophile species.

Keywords

Cave, ethology, morphology, planthoppers, wax plates, wing venation

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Introduction

As obligate phytophagous insects, planthoppers (Hemiptera, Fulgoromorpha) would not be expected to live in caves. However, the root system of the aerial vegetation offers root-feeding planthoppers the opportunity to eventually adapt and evolve in temporary, cyclical or even permanent hypogean conditions. Since the first report by Racovitza (1907), more than 60 planthopper species in five planthoppers families (Cixiidae Spinola, 1839, Delphacidae Leach, 1815, Meenoplidae Fieber, 1872, Kinnaridae Muir, 1925, and Hypochthonellidae China & Fennah, 1952), have been reported living exclusively in the subterranean ecosystems (Hoch 1994; Hoch 2013, and references therein; FLOW 2022). According to their biology, they have been classified as true cavernicolous species or troglobionts, eutroglophiles (species able to maintain permanent hypogean populations), subtroglophiles (species living temporally or cyclically in hypogean conditions) and trogloxenes (species occurring sporadically in a hypogean habitats, unable to establish subterranean stable populations) (Sket 2008; Howarth and Moldovan 2018).

Although several hypogean species have been reported from the Macaronesian islands (Canary Islands, Azores, Cape Verde) and the Baleares (Mallorca: unconfirmed record; Racovitza 1907), in continental Europe, true cavernicolous species remain exceptional. One species of Kinnaridae, *Valenciolenda fadaforesta* Hoch & Sendra, 2021, was recently described from two karstic caves of the Iberian Mountain Range in Spain (Hoch et al. 2021). The other two are Cixiidae Cixiini: *Ibleocixius dunae* D'Urso & Grasso, 2009, described from Sicily from a limestone cave (d'Urso and Grasso 2009) and *Trirhacus helenae* Hoch, 2013, from a dolomite cave in Mljet island, Croatia (Hoch 2013). In the adult stage, they all have more or less strong morphological adaptations to underground life and as troglobionts, they are are adapted to the stabilize conditions they experience underground.

Only few planthoppers are considered eutroglophiles and subtroglophiles, which are less strongly linked to hypogenous habitats (FLOW 2022). In Europe, another Oecleini monotypic cixiid genus, *Trigonocranus* Fieber, 1875 with the species *Trigonocranus emmeae* Fieber, 1876, should be regarded as a subtroglophilic species (Hoch et al. 2013). It is a rarely collected species known from few localities in northern parts of western Europe and Russia and seems to inhabit the interstitial ground level. Adults often exhibit varying degrees of certain troglomorphies such as reduction of the compound eyes, wings and weak pigmentation (Hoch et al. 2013).

Following Emeljanov's subdivisions (2002), the classification of the Cixiidae was recently reviewed by Luo et al. (2021) who recognized three main lineages (but without formal rank while awaiting further phylogenetical analysis): the oecleine lineage (including Duiliini Emeljanov, 2002, Cajetini Emeljano, 2002, Stenophlepsini Metcalf, 1938, Oecleini Muir, 1922, and Bothriocerini Muir, 1923 downgraded from subfamilial rank), sister to a pentastirine (with Pentastirini Emeljanov, 1971 and perhaps Borysthenini Emeljanov, 1989, downgraded from subfamilial rank) and

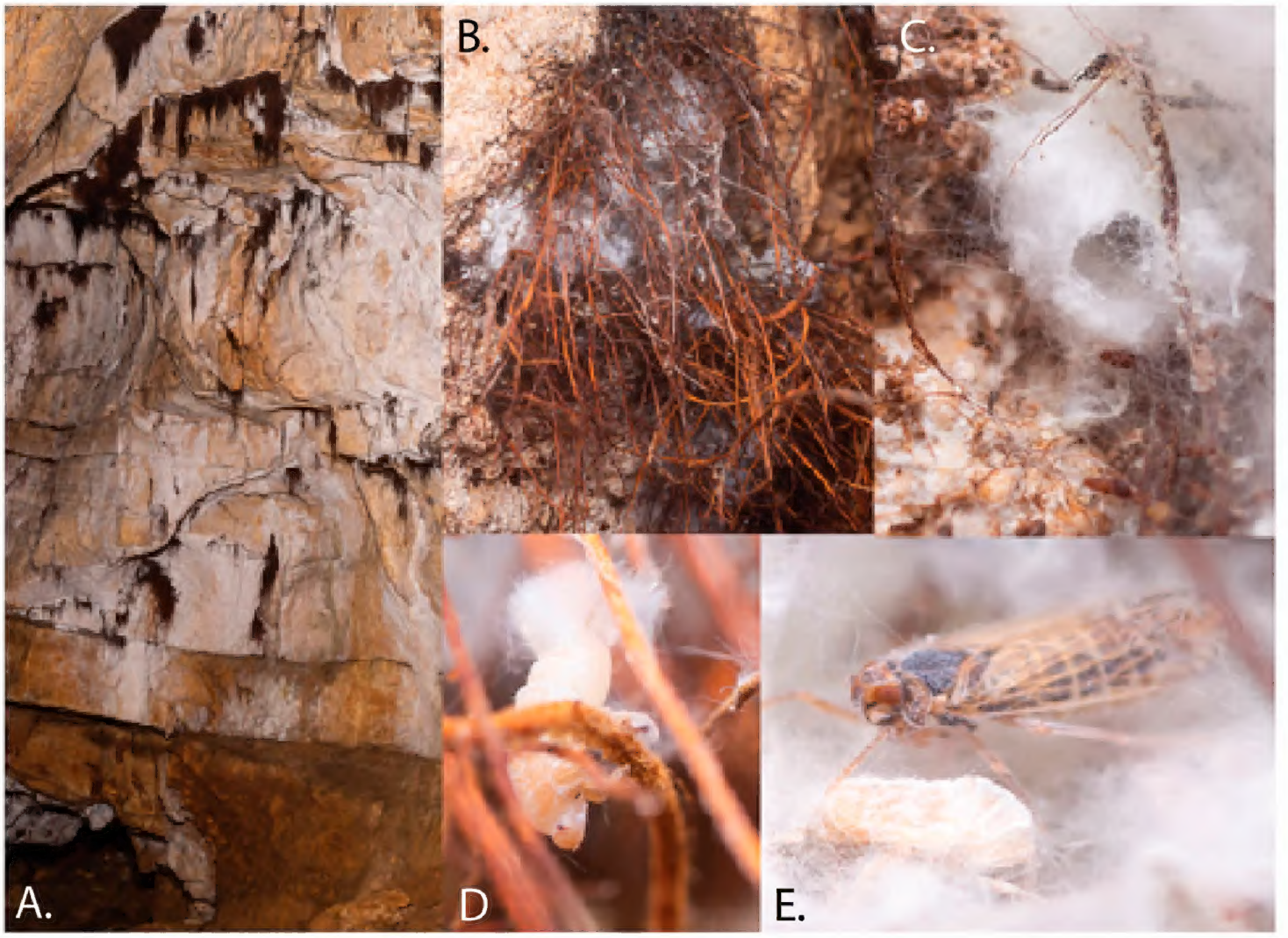

Figure 1. *Coframalaxius bletteryi* in its natural habitat **A** cave with roots **B** roots with cixiid nests characterized by the waxy filaments left by the nymphs **C** waxy galleries where nymphs and adults were observed **D** fifth instar nymph feeding on rootlet **E** adult and nymph inside nest.

a cixiine lineage (including all other cixiid tribes). Three tribes were not addressed by Emeljanov (2002): Gelastocephalini Emeljanov, 2000, Mnemosynini Emeljanov, 1992 and Benarellini Emeljanov, 1989). In this paper, we describe a new genus of Cixiidae in the tribe Oecleini, for a new species recently discovered in a cave in southern France. A molecular analysis confirms its placement in the Oecleini. This species has the classic nymphal troglomorphies present in most species of the family and adults look like typical epigeal species. However this planthopper has never been observed in any habitat above ground, even though the area where the cave is located has been well investigated with respect to its epigean fauna over many years. Accordingly, the ecological classification of the new species is discussed.

Materials and methods

Specimens were collected by hand with an aspirator and killed in cyanide jars. All specimens are stored dried on cardboard in the Muséum national d'Histoire naturelle, Paris, France (MNHN). Each label under a specimen is reported between brackets:

[label1][label2]... For descriptive purposes, entire nymphs or adult abdomens were boiled in 10% NaOH solution for a few minutes. Residual endodermic soft tissues were removed in distilled water before transferring the whole abdomen into glycerin for dissection and observation. Dissected nymphs, abdomen parts and genitalia were stored under their related specimens in genitalia vials in a drop of glycerin for final conservation. Preparation and observation of specimens were done under a Leica MZ12.5 stereo microscope. Photos were taken either with the adapted module Leica IC90E and Leica Acquire software (version 2.4.6 Build 9112), either with a Canon EOS 6D with a Macrolens Canon EF 100 mm f/2.8, and then assembled with the software Helicon focus 6.

Morphological terminology for male genitalia follows Bourgoin (1988), for female genitalia Bourgoin (1993), and forewing venation Bourgoin et al. (2015). Terminology of vertex is adapted from Loecker (2014: Fig.1) and follows Fig. 2. The metatibiotarsal formula lT-(aTd)/aI/aII corresponds to the number of lateral (lT) and apical teeth (aT) on the metatibia, eventually with a diastema (d), the number

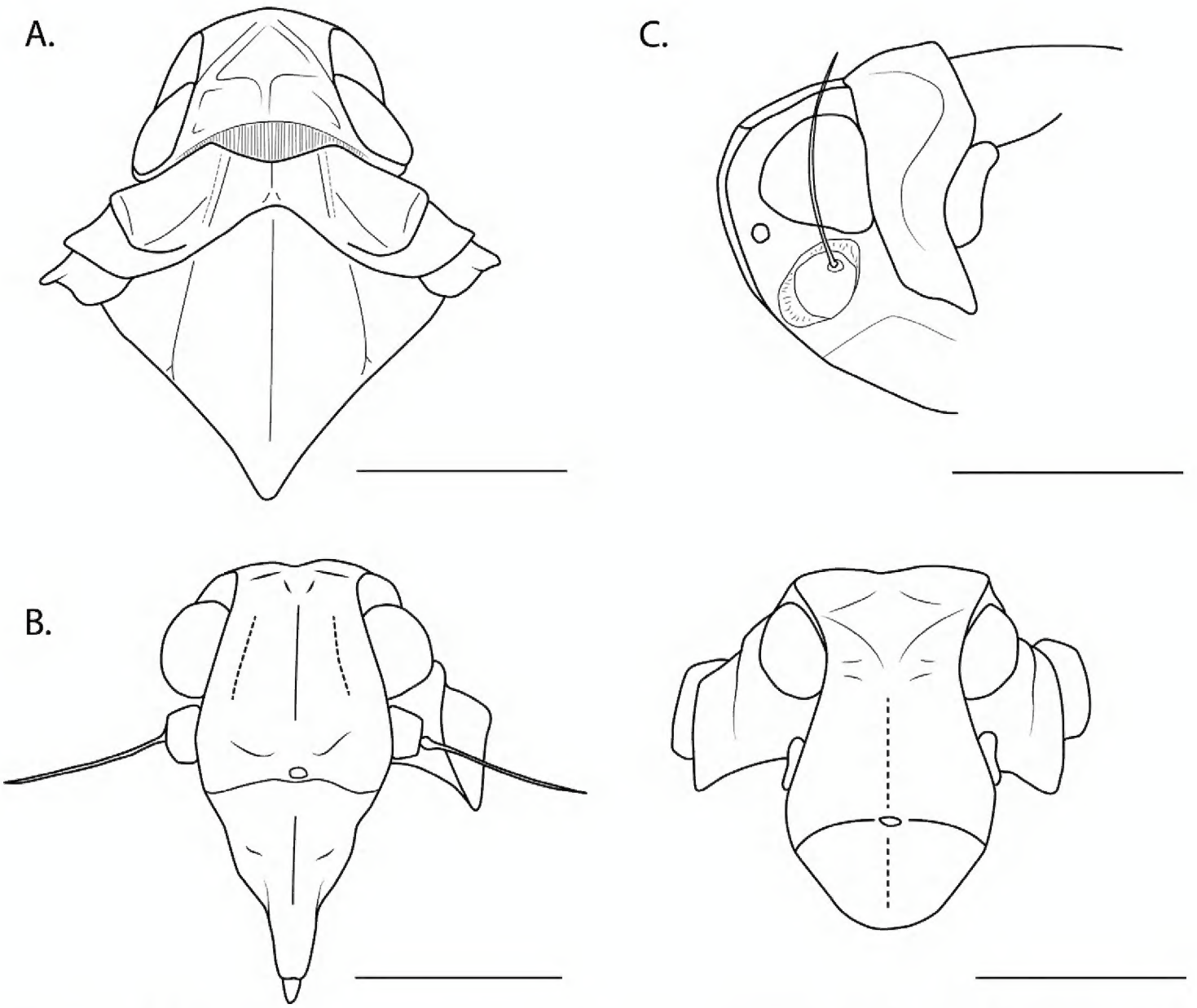

Figure 2. *Coframalaxius bletteryi* gen. et sp. nov. head capsule **A** dorsal **B** frontal **C** dorsofrontal and lateral view. Scale bar: 0.5 mm.

of apical teeth (aI) on metatarsomere I, and the number of apical teeth (aII) on metatarsomere II.

Total genomic DNA was extracted from legs muscle tissue using the Qiagen DNEasy kit (Qiagen, Inc., Valencia, CA, USA). Analyses were conducted on partial sequences of *18SrDNA* (1939 bp; first third of the gene not sequenced), *28SrDNA* (D3-D10; 3057 bp), cytochrome oxydase I (*COI*; 1239 bp), cytochrome b (*Cytb*; 426 bp), and histone 2A (*H2A*; 306 bp). Oligonucleotide primers used for polymerase chain reaction (PCR) amplification are listed in Table 1. The full dataset includes 37 taxa: 3 delphacids as out-group taxa and 34 ingroup taxa representing all three subfamilies of the Cixiidae (Borystheninae, Bothriocerinae, Cixiinae). All species available to us from the oeclinian lineage *sec.* Luo et al. 2021, were included; 29 species were directly available from Genebank of which we added 8 new samples. All related registration numbers in GenBank are provided in Table 2.

Phylogenetic reconstruction using maximum likelihood (ML) was generated in Phylip formats using PhyloSuite V1.2.1 (Zhang et al. 2020). The best partitioning scheme and replacement model were selected by PartitionFinder V2.0.0 (Lanfear et al. 2016), resulting in 9 partitions fitting 6 best models (Table 3). Maximum likehood (ML) analysis were carried out with IQTREE V1.6.8 (Guindon et al. 2010; Minh et al. 2013; Nguyen et al. 2015). The resulting topology was prepared with iTOL v5 (Letunic and Bork 2021).

Table 1. Primer sequences used for the molecular analysis.

Primer	Sequence (5' – 3')	Primer Source
COI		
2183 (F)	CAACATTTATTTTGATTTTTTGG	Simon et al. (1994)
UEA8 (R)	AAAAATGTTGAGGGAAAAATGTTA	Lunt et al. (1996)
Cytb		
CB1 (F)	TATGTACTACCATGAGGACAAATATC	Jermiin and Crozier (1994)
CP2 (R)	CTAATGCAATAACTCCTCC	Harry et al. (1998)
18S rDNA		
574 (F)	GCCGCGGTAATTCCAGCT	Bourgoin et al. (1997)
E21 (R)	CTCCACCAACTAAGAACGG	
18S–mid (F)	GATACCGCCCTAGTTCTAACC	
2200 (R)	CGGCAGGTTCACCTACGG	
28S rDNA		
Ai (F)	GACCCGTCTTGAAACACG	Litvaitis et al. (1994)
D4D5r (R)	GTTACACACTCCTTAGCGGA	Belshaw and Quicke (2002)
EE (F)	CCGCTAAGGAGTGTGTAA	Cryan et al. 2000
MM (R)	GAAGTTACGGATCTARTTTG	
Lalt (F)	CCTCGGACCTTGAAAATCC	Dietrich et al. 2001, as 'fragment IV
Galt (R)	TGTCTCCTTACAGTGCCAGA	
V (F)	GTAGCCAAATGCCTCGTCA	Cryan et al. 2000
X (R)	CACAATGATAGGAAGAGCC	
H2A		
F1 (F)	TGTCTGGYCGCGGCAARGG	Cryan & Urban, 2011
R1 (R)	ACGGCCTGGATGTTGGGCA	

Table 2. Investigated species, with their main distribution and registration numbers of sequenced genes. New sequences are marked with (*).

Species	Distribution	*COI*	*Cytb*	*18S*	*28S*	*H2A*
Cixiidae						
Achaemenes intersparsus Jacobi, 1907	Madagascar	EU183598	–	EU183575	EU183704	–
Borbonomyndus pandanicola Attié, Bourgoin & Bonfils, 2002	Reunion Island	EU183593	–	EU183571	EU183735	–
Borysthenes sp. *	China: Hunan	ON079066	ON113340	ON087638	ON130260	–
Bothriocera eborea Fennah, 1943	US Virgin Island	EU645971	–	DQ532511	DQ532591	JN797395
Bothriocera sp.1	Martinique	EU183603	EU183642	EU183577	EU183670	–
Bothriocera sp.2	Belize	EU183604	–	EU183581	EU183675	–
Coframalaxius bletteryi gen. et sp. nov. *	France	ON087562	ON113342	ON087640	ON231299	ON101633
Colvanalia sp. *	China: Zhejiang	–	OK169309	MW306541	–	–
Cixius bicolor Matsumura, 1914 *	China: Taiwan	–	OK169315	MW306536	MW306556	ON101626
Cixius sp. *	China: Shaanxi	MW291679	ON152767	MW306516	MW306544	OK169342
Colvanalia taffini Bonfils, 1983	Vanuatu	EU183613	–	EU183560	EU183690	–
Haplaxius crudus (Van Duzee, 1907)	USA (FL)	EU183606	–	EU183553	EU183680	–
Haplaxius deleter (Kramer, 1979)	Costa Rica	EU183605	EU183631	EU183552	EU183679	–
Haplaxius delta (Kramer, 1979)	Costa Rica	MT900602	–	MT892908	–	–
Haplaxius dougwalshi Bahder et al., 2020	Costa Rica	MT080284	–	MT002395	–	–
Haplaxius lunatus (Van Duzee, 1909)	USA (FL)	OM264285	–	OM258692	–	–
Haplaxius pictifrons (Stål, 1802)	Costa Rica	MT946292	–	MN200098	–	–
Haplaxius sp.	Costa Rica	MW086873	–	MW086509	–	–
Haplaxius skarphion (Kramer, 1979)	Mexico	–	–	EU183570	EU183682	–
Meenocixius virescens Attié, Bourgoin & Bonfils, 2002	Reunion Island	EU183614	EU183639	EU183572	EU183736	–
Myxia baynardi Bahder & Bartlett, 2021	Costa Rica	MT900604	–	MT892909	–	–
Myxia belinda Bahder & Bartlett, 2020	Costa Rica	MT900605	–	MN200096	–	–
Myxia hernandezi Bahder & Bartlett, 2021	Costa Rica	MZ234085	–	MZ262449	–	–
Nymphocixia caribbea Fennah, 1971	Cuba	EU183615	–	EU183561	–	–
Nymphocixia unipunctata Van Duzee, 1923	USA (FL)	OM264284	–	OM258690	–	–
Oecleopsis tiantaiensis Guo, Wang & feng, 2009 *	China: Hunan	MW291684	–	MW306535	MW306590	–
Oecleus mackaspringi Myrie et al., 2019	Jamaica	MN488999	–	MN422261	–	–
Oecleus perpictus Van Duzee, 1929	USA(AZ)	–	–	JQ982515	JQ982532	–
Oecleus productus Metcalf, 1923	USA	–	EU183647	–	EU183719	–
Oecleus sp.2	USA (UT)	EU645972		DQ532512	DQ532592	–
Oecleus sp.1	Belize	–	EU183649	–	EU183662	–
Oliarus sp. *	China: Guizhou	MW291688	–	MW306513	MW306564	–
Pintalia alta Osborn, 1935	US Virgin Island	–	–	AY744804	AY744838	–
Trigonocranus emmae Fieber, 1876 *	Belgium	–	–	ON260952	–	–
Delphacidae						
Asiraca clavicornis (Fabricius, 1794)	Kyrgyzstan	AF304409	–	HM017281	HM017389	–
Kelisia curvata Beamer, 1954	USA(PA)	–	–	HM017235	HM017343	–
Ugyops stigmata (Crawford, 1914)	Belize	HM017501	–	HM017301	HM017409	–

Table 3. Best partitioning schemes and models for maximum likelihood (ML) analysis.

Genes/codons in partition	Model in IQtree
COI, 18S and 28S	GTR+I+G
nt1 of H2A	GTR+I
nt1 of Cytb	GTR+G
nt2 and nt3 of Cytb	K81UF+I+G
nt3 of H2A	K81UF+G
nt2 of H2A	K81

Taxonomy

Hemiptera Linnaeus, 1758
Cixiidae Spinola, 1839
Cixiinae Spinola, 1839
Oecleini Muir, 1922

***Coframalaxius* Bourgoin & Le Cesne, gen. nov.**
http://zoobank.org/978AA57A-FCE2-45DC-8512-E555F327B1B

Type species. Coframalaxius bletteryi Le Cesne & Bourgoin (by present designation and monotypy).

Etymology. Arbitrary combination of the first syllabus of author (T. Bourgoin) four grandsons with suffix -xius from *Cixius*, type genus of the family Cixiidae.

Diagnosis. Small cixiids, in habitus resembling *Trigonocranus* Fieber, 1875, but can be distinguished from the latter by the combination of the following characters: 1) pygofer longer in lateral view, expanded in a triangular lobe on its latero-posterior margin, 2) anal tube with proximal pair of lateroventral teeth, 3) posterior part of gonostyli wider and 4) aedeagus with one internal spine-like process. Female pygofer elongated, without wax plates.

Description. ***Head capsule.*** Vertex with posterior compartment sub-rectangular, anterior compartment triangular; subapical carina straight weakly marked, apical carina well distinct, median carina weak vanishing at subapical carina level; in lateral view, slightly surpassing lateral carina. Frons wider at ventral level of antennae in frontal view; frontoclypeal suture slightly arched dorsally, median carina weak, distinct only in dorsal part and not reaching median ocellus; in lateral view, regularly convex, slightly surpassing laterofrontal carina. Postclypeus with lateral margins slightly concave in basal 1/3; in frontal view, median carina weak in ventral 2/3. Anteclypeus lacking median carina. Compound eye thinly elongated in dorsal view. Antennal socket wide, emarginated, almost touching ventral margin of compound eye; scape short, pedicel globular with distinct transversal margin in frontal view, flagellum with basal swelling well developed, almost five times as long as pedicel, surpassing in length the level of lateral side of abdomen (Fig. 2). Lateral ocelli present, separated from compound eye by

1X their length. Labium almost reaching metacoxae; apical segment 1/4 length of subapical one, slightly thinner medially, proximal segment half as long as subapical one.

Thorax. Prothorax anterior margin widely roundly concave (Fig. 2); posterior margin more sharply roundly concave (Fig. 2); median carina present, not reaching posterior margin; postocular carinae well distinct, not meeting posterior margin and running subapically to its ventral margin in frontal view (Fig. 2B, C). Mesonotum tricarinate with median and lateral carinae. Forewing elongated; stem ScP+R+MP slightly longer than basal cell length, forking at 1/4 of forewing length, before level of PCu+A1 fusion; anterior and posterior margins subparallel. C1 cell distinctly curved; anterior branch of MP (MP_{1+2}) forking twice: in MP_1 and MP_2, then MP_{1a}, and MP_{1b}. Posterior branch MP_{3+4} single, unforked. C5 cell short, diamond-shaped, ending with CuA_1+CuA_2 fused; icu reaching apex of clavus (Fig. 3A). Hindwing with MP and CuA connecting in I-type (Fig. 3C).

Hindleg with metatibia laterally unarmed, with 6 apical teeth separated in two groups of 3 by a wide diastema, and outermost tooth largest; first metatarsomere elongate, not dilated apically, with 8–9 apical teeth; second metatarsomere with (7–8) apical teeth, without setae under the first one or two teeth on each side, with one long straight setae under the three to five medium teeth; metatibitarsal formula: 0-(3d3)/(8–9)/(7–8)

Male genitalia. Anal tube symmetrical, with an anterior pair of lateroventral conspicuous hook-like spines. Pygofer symmetrical, dorsocaudally produced into a triangular lobe; suspensorium developed, X-shaped, attached to ventral margin of anal

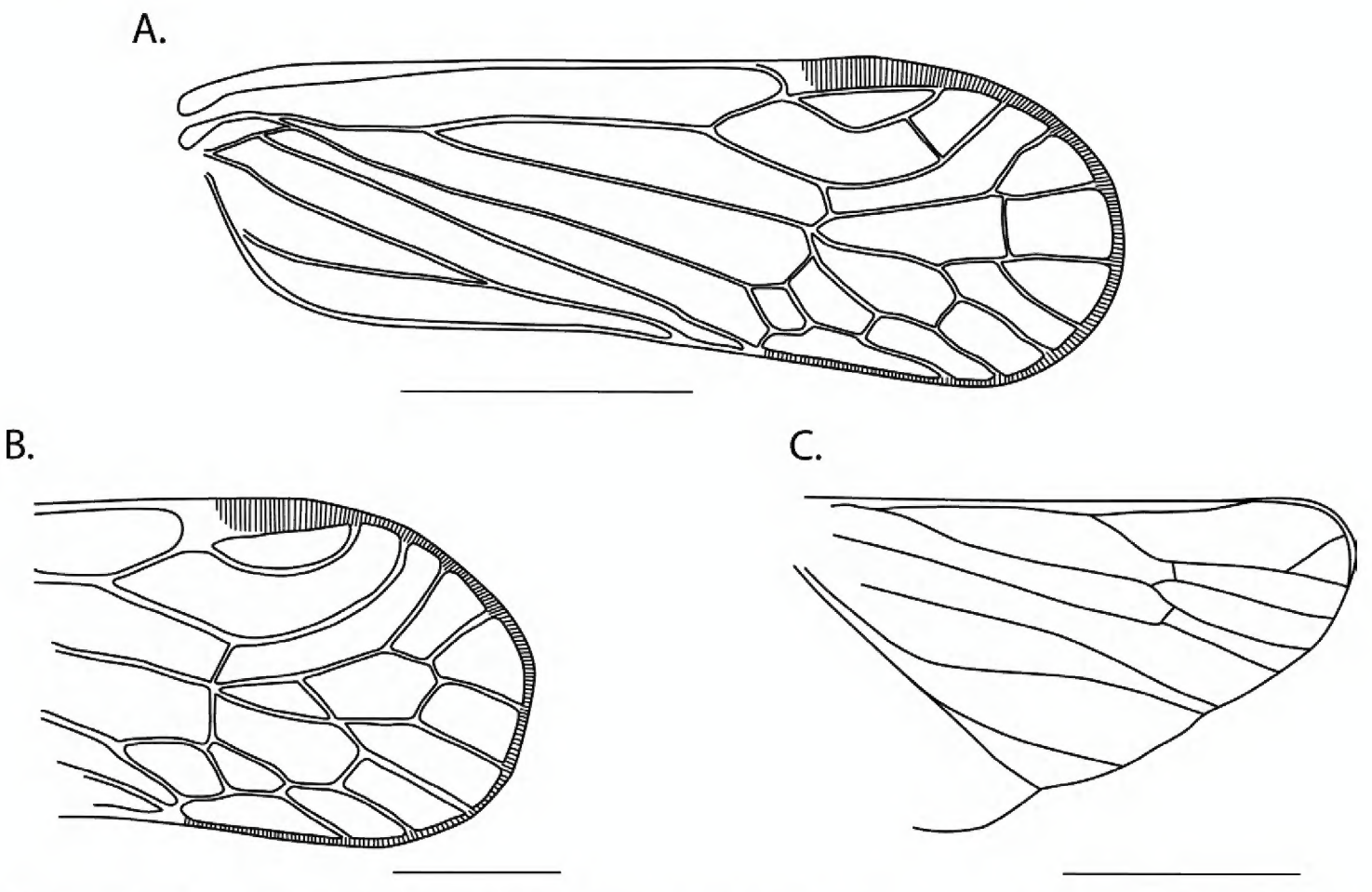

Figure 3. Wings of *Coframalaxius bletteryi* gen. et sp. nov. **A** tegmina venation pattern **B** variation of tegmina venation **C** hind wing venation pattern. Scale bars: 1 mm (**A, C**); 0.5 mm (**B**).

tube (Fig. 4). Male copulatory organ with periandrium tube-like, elongated, bearing spines and processes. Aedeagus s.s. very short, endosoma not or very shortly developed. Gonostyli bilaterally symmetrical, with proximal portion slender, apically developed into a spoon-shaped extension with a nearly pentagonal outline, directed dorsally.

Female genitalia of orthopteroid type, sword-shaped ovipositor, following paired hemisternite VII medially divided by a membranous portion (Fig. 5). Pygofer of elongated type without ventral wax plate. Gonoplac fused, apically separated. Ductus receptaculi regular, short, not developed in a helix-twirled structure (Fig. 5C).

Nymphs. Two short laterometatibial spines in 5th instar (Fig. 6). With abdominal paired tergal wax plates on tergites VI to VIII divided into 6 subplates separated by one sensory pits, those ones ranged in raw in subanterior position (Fig. 6). In instars 3 to 5: procoxa with one sharp anterior process bearing small (sensorial?) dark triangular microcuticular sculptures; profemur with a conspicuous latero-extern process bearing a row of short sensorial setae-like structures, protibia short distally truncate, bearing two tarsomeres.

Coframalaxius bletteryi **Le Cesne & Bourgoin, sp. nov.**
http://zoobank.org/BF08E58D-256F-4286-9CEB-4A87A736D384

Genebank registration. ON087562/ ON113342/ ON087640/ ON231299/ ON101633.

Etymology. Dedicated to Jonathan Blettery who discovered the first specimen during a fieldtrip with the two first authors exploring caves around Nice in the south of France.

Diagnosis. Small species externally similar to *Trigonocranus emmeae* Fieber, 1876, from which it can easily be separated by the triangular areolet of the vertex (versus pentagonal (Emeljanov 2015: 69 and fig.21.6) in *T. emmeae*), but also by the rounded posterior margin of the pronotum (versus angular), the conformation of the male genitalia with thinner spiniform processes also different in number and conformation and particularly by a unique internal distinct process inside the periandrium (Fig. 4).

Color. Compound eyes, post clypeus, areolet, anterior part of prothorax behind vertex and mesonotum black, frons paler and carinae yellowish-brown. Tegmina translucent without color patches, pterostigma and vein pale brown, with setiferous granules darker; veins after nodal line darker. Legs pale brown. Metatibia and metatarsomere teeth black, median spines of metarsormere II with setae paler.

Male terminalia with anal tube regularly ovoid, in dorsal view more or less regularly convex lateroventrally in lateral view with a pair of lateroventral teeth directed posteroventral. Male genitalia asymmetrical with suspensorium X-like, connected to the perandrium basally shortly wide then distally tube-like; bearing 5 spiniform processes: a very basal and dorsal short straight spiniform process (1), on left side a long proximal spiniform process directed dorsoposteriorly then bent posteroventrally (2), a short acute ventral process (3), an elongate dorsal spiniform process forked at mid length in a short teeth-like (4) and a short internal hook-like process, located inside the

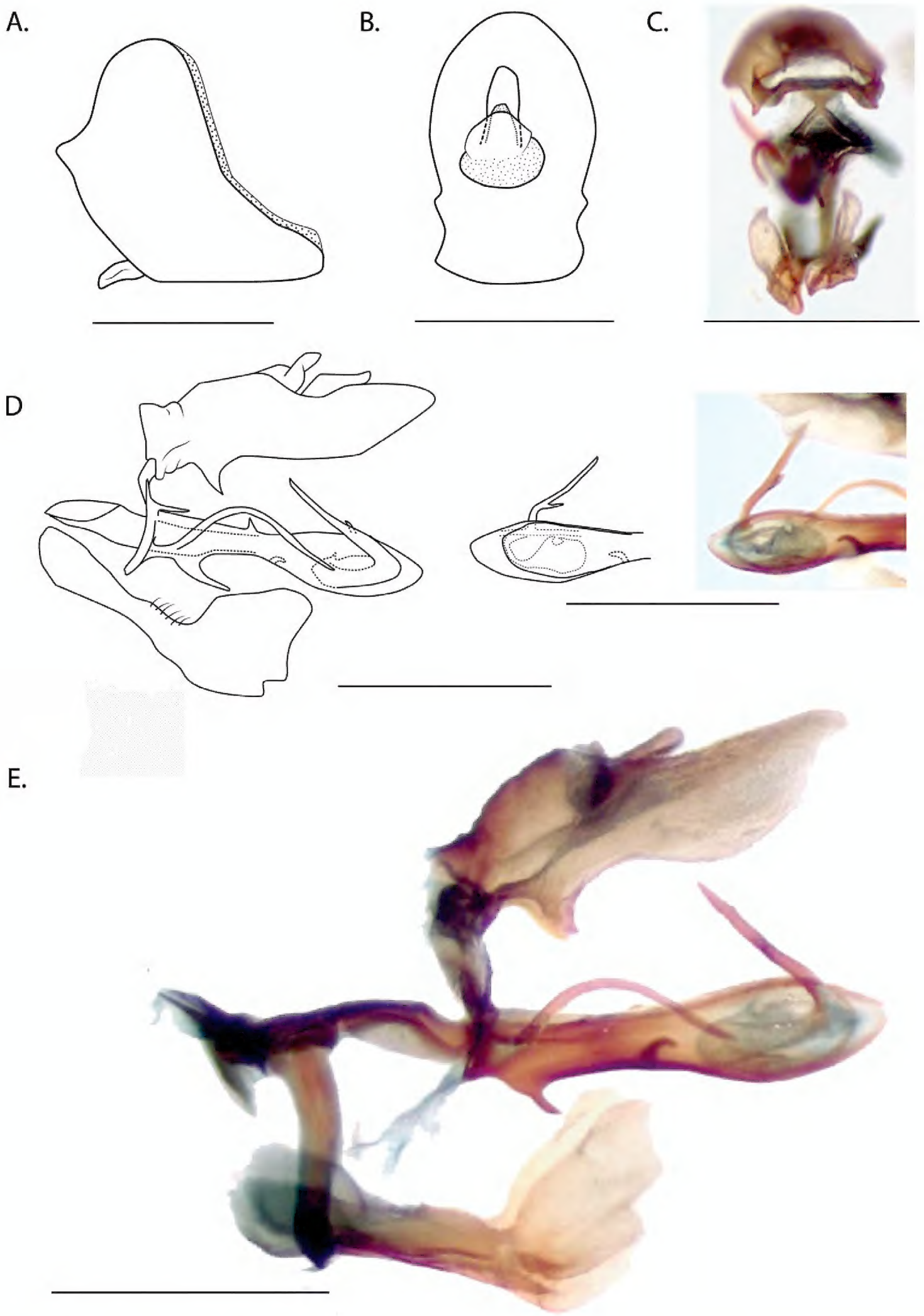

Figure 4. *Coframalaxius bletteryi* gen. et sp. nov. Male genitalia **A** pygofer lateral view **B** anal tube, dorsal view **C** suspensorium **D, E** male genitalia left lateral view **F, G** male genitalia apex, right side. Scale bar: 0.5 mm.

periandrium (5). Gonopore opening large on apical right side, endosoma not visible, probably very weakly developed.

Female terminalia (Fig. 5) with paired sternite VI; each gonocoxa VIII developed in a wide plate slightly bilobed lateroapically; gonapophyses IX fused, slightly larger than gonapophyses VIII; gonapophyses VIII larger proximally in a wide triangular endogonocoxal lobe; gonoplacs longer than gonapophyses and enveloping them.

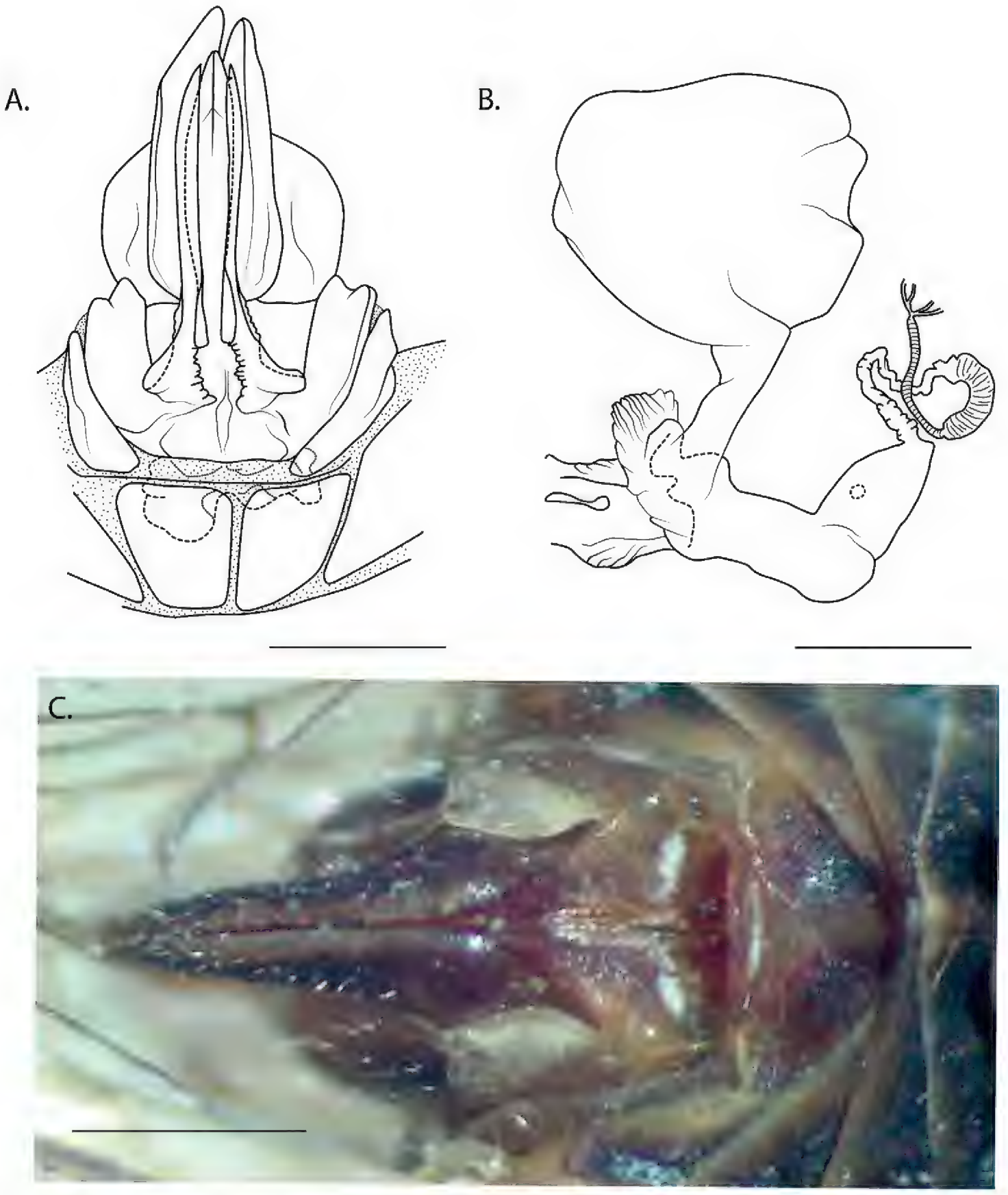

Figure 5. *Coframalaxius bletteryi* gen. et sp. nov. Female genitalia **A, B** ventral view **C** ectodermal internal ducts of female genitalia. Scale bar: 0.5 mm.

Opening of ectodermic internal parts with developed lateral swellings of vestibulum, opening into posterior vagina developed in a strong wrinkled membranous pouch on left side, opening dorsally into the ductus bursae leading to a membranous translucent bursa copulatrix, and laterally into the anterior vagina bent at mid length and ending in the spermatheca; spermatheca with pars intermedialis, half-length of anterior vagina, opening into a diverticulum ductus bent, followed by a long pars intermedialis before vanishing into the the mesodermic glandula apicalis.

Material type. ***Holotype*** male, pinned, original description: [Grotte de la chèvre d'or; Roquefort-less-Pins; France (06)], [12-VII-2021; J. Blettery rec.], [*Coframalaxius bletteryi* Le Cesne & Bourgoin sp. nov.; M. Le Cesne det. 2022], [MNHN(EH) 24997].

***Paratypes*:** 1 female, pinned, with genitalia in a separate microvial, original label: [Grotte de la chèvre d'or; Roquefort-les-Pins; France (06)], [*Coframalaxius bletteryi* Le Cesne & Bourgoin sp. nov.; M. Le Cesne det. 2022], [MUSEUM PARIS; 12-VII-2021; T. Bourgoin rec.], [Museum Paris; MNHN(EH) 24998] ; 4 females, pinned, original label: [France, 06; Roquefort-les-Pins; grotte de la chèvre d'or],[MUSEUM PARIS; 12-

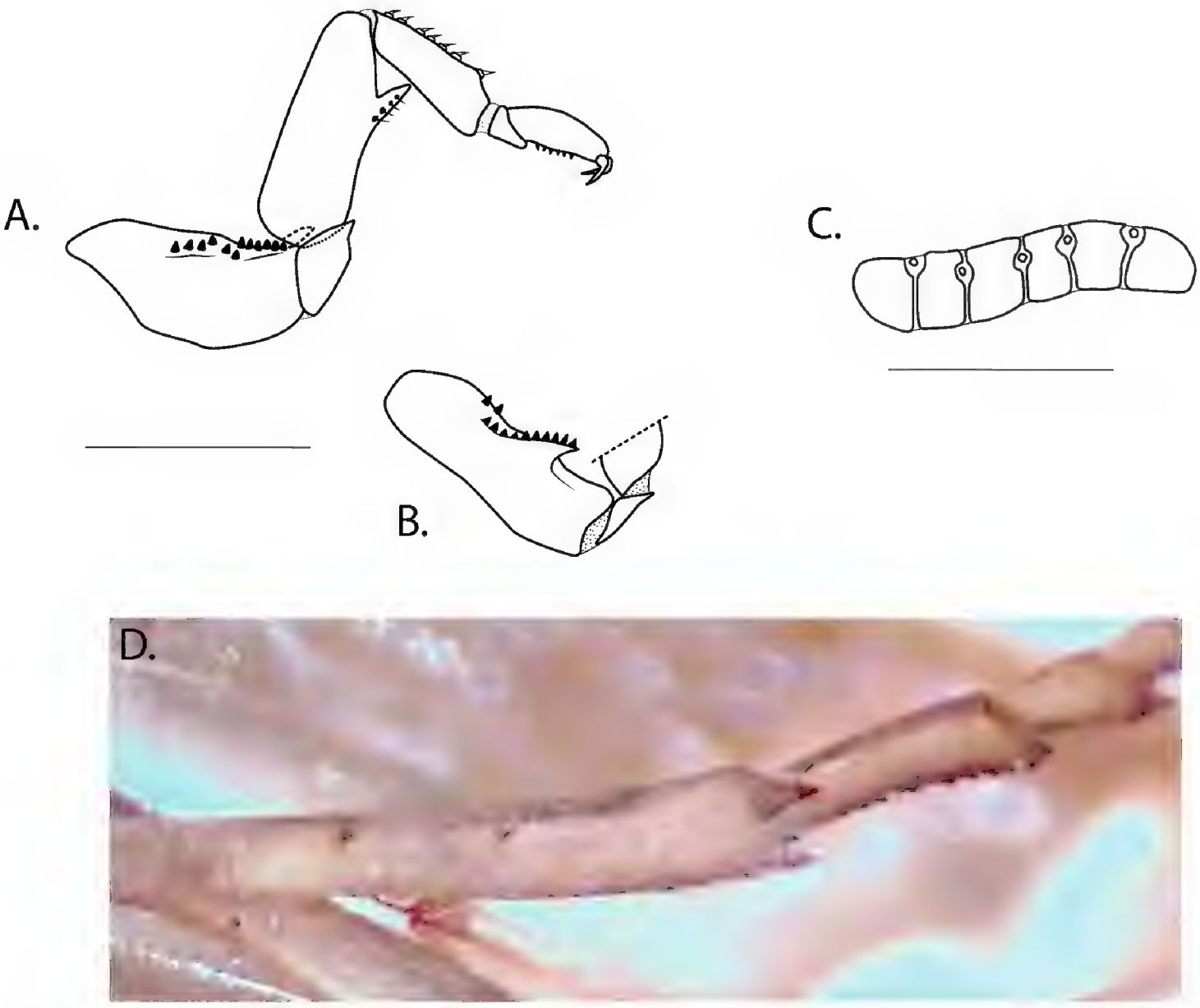

Figure 6. *Coframalaxius bletteryi* gen. et sp. nov. Fifth instar nymp **A, B** proleg, ventral view and anteroventral view **C** Sternite VI, wax plates. Scale bar: 0.5 mm.

VII-2021; T. Bourgoin rec.], [*Coframalaxius bletteryi* Le Cesne & Bourgoin sp. nov.; M. Le Cesne det. 2022], [Museum Paris; MNHN(EH) 25177, 25178, 25179, 25180] ; 2 males, pinned, with genitalia in a separate microvial, original label: [France, 06; Roquefort-les-Pins; grotte de la chèvre d'or],[MUSEUM PARIS; 17-VII-2021; M. Le Cesne rec.], [*Coframalaxius bletteryi* Le Cesne & Bourgoin sp. nov.; M. Le Cesne det. 2022], [Museum Paris; MNHN(EH) 25181, 25182] ; 3 males, pinned, original label: [France,

Figure 7. *Coframalaxius bletteryi* gen. et sp. nov. Habitus photos.

06; Roquefort-les-Pins; grotte de la chèvre d'or],[MUSEUM PARIS; 12-VII-2021; T. Bourgoin rec.], [*Coframalaxius bletteryi* Le Cesne & Bourgoin sp. nov.; M. Le Cesne det. 2022], [Museum Paris; MNHN(EH) 25183, 25184, 25185] ; 3 males, pinned, original label: [France, 06; Roquefort-les-Pins; grotte de la chèvre d'or],[MUSEUM PARIS; 12-VII-2021; J. Blettery rec.], [*Coframalaxius bletteryi* Le Cesne & Bourgoin sp. nov.; M. Le Cesne det. 2022], [Museum Paris; MNHN(EH) 25186, 25187, 25188].

Other material. Several other nymphs at various instars, pinned.

Type locality. Roquefort-les-Pins, Alpes-Maritimes, France

Phylogeny. *Coframalaxius bletteryi* was sequenced for: COI, Cytb, H2A, 18S and 28S (D3-D5, D6-D7), but only successfully sequenced for 28S (D6-D7) for *Trigonocranus emmeae.* Comparison between the two taxa shows significant differences in both total characters and base frequencies, that differs by 37 characters (4.4%) (Table 4). The resulting topology of the molecular analysis (Fig. 8) confirms the placement of *Coframalaxius* into Oecleini as sister to *Trigonocranus.*

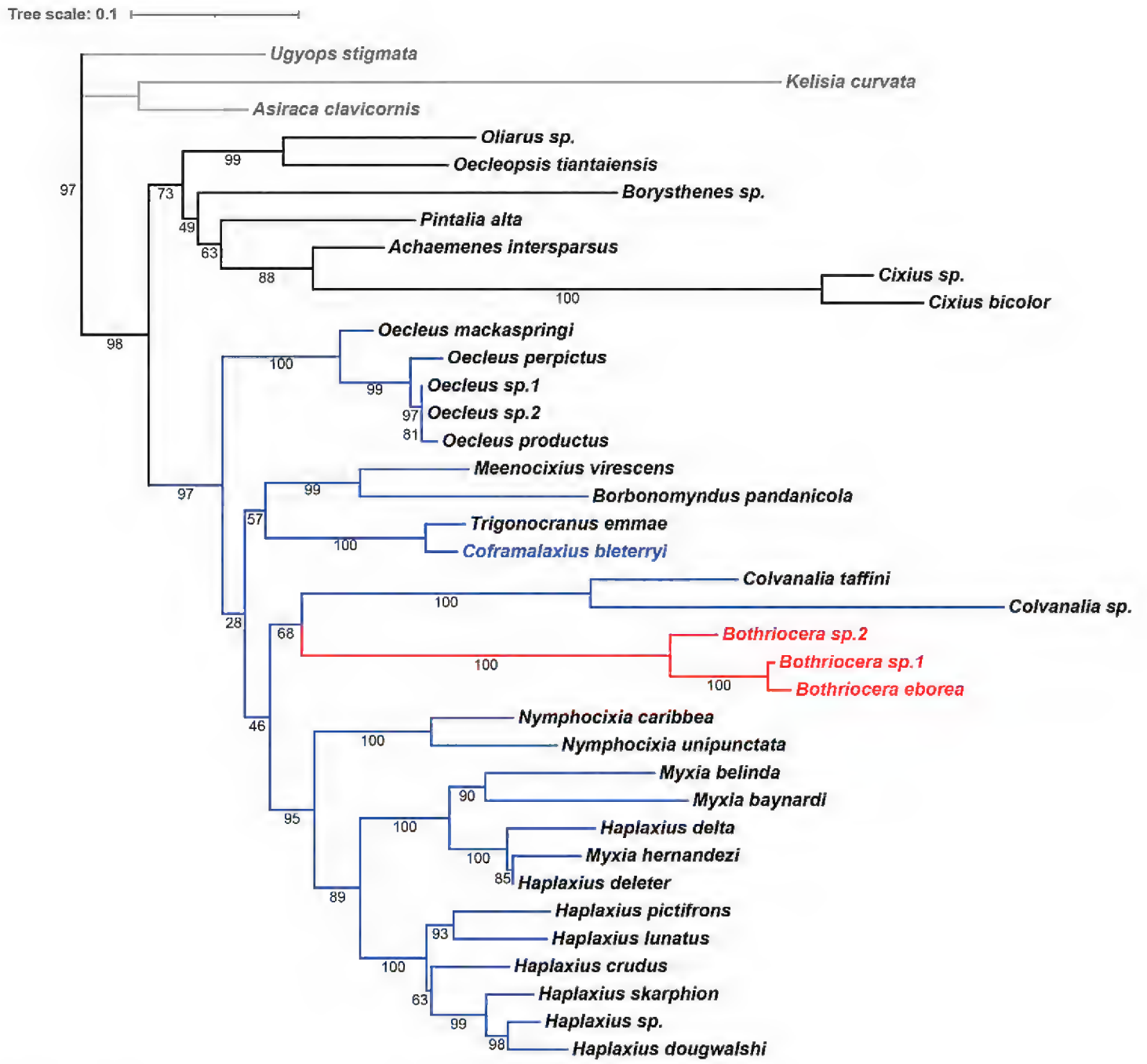

Figure 8. *Coframalaxius* placement within Cixiidae by molecular phylogeny analysis. Out-groups in grey, Oecleini in blue, Bothriocerini in red. Node labels provide UFBoot support values.

Table 4. Summary of the sequence information of 28S (D6-D7) of *Trigonocranus* and *Coframalaxius*.

28S (D6-D7)	Total characters	Base frequencies (%)			
		A	C	G	T
Trigonocranus emmeae	837	21.4	25.9	32.9	19.8
Coframalaxius bletteryi	830	21.6	25.1	33.1	19.4

Discussion

1. *Coframalaxius* classification in the Cixiidae Oecleini

According to Emeljanov's 2002 classification, *Coframalaxius* can be excluded from the pentastirinian and cixiinian lineage (Luo et al. 2021) based on the presence of paired sternite VIII in males (*versus* unpaired), icu joining apex of clavus (*versus* displaced distal to apex of clavus), the laterally unarmed metatibia with the presence of a metatibial diastema (*versus* a more or less regular line of teeth), and an elongated female genitalia (*versus* reduced or short). All these characters, together with the head capsule conformation distinctly different from the Bothriocerini type, places the new genus within the Oecleini.

The placement of *Coframalaxius* in Oecleini is also confirmed by the molecular phylogeny analysis (Fig. 8) which puts it relatively close to its basal node in a strongly supported Palaearctic clade with *Trigonocranus*, both being sister to a La Reunion clade grouping *Borbonomyndus* Attié, Bourgoin & Bonfils, 2002, and *Meenocixius* Attié, Bourgoin & Bonfils, 2002. If the oecleine lineage appears well supported, the basal branching of the different groups of taxa (including Bothriocerini) remain weak and need further analysis, which is beyond the scope of this paper. Interestingly, the separation between the two genera *Haplaxius* Fowler, 1904 and the recently described *Myxia* Bahder & Bartlett, 2019, also needs more investigation. However, only 9 out of 25 curently recognized oecleine genera are present in the phylogenetic analysis. In particular, the genus *Myndus* Stål, 1862 is not represented, whereas, with its worldwide distributed 81 species (Bourgoin, 2022), it very probably represents a paraphyletic unit.

Our phylogenetic analysis posits a paraphyletic Oecleini, including Bothriocerini, rather than a sister relationship between the two tribes as suggested by Emeljanov (2002). However, the phylogenetic relationships of the oecline lineage and more specifically within the Oecleini (*s. l.*) will be addressed in another paper (Luo et al. in prep).

2. Morphological characters in support of placement of *Coframalaxius* into Oecleini

Nymphal prolegs

Myers (1929) first described the fossorial prolegs of the fifth instar of *Bothriocera signoretti* Stål, 1864 as did Wilson and Tsai (1982) and Wilson et al. (1983) of the fifth instars of the oecleines *Haplaxius crudus* (Van Duzee, 1907) and *Oecleus borealis* Van Duzee, 1912. Emeljanov (2002) mentioned the "thick and dentate fossorial forelegs" in nymphs as a possible characteristic of Bothriocerini, Oecleini, and probably Cajetini (because of their

unique thick adult forelegs). Subsequently with his figure (Emeljanov 2002: fig. 12), he implied inclusion of Stenophepsiini in this group of tribes, but not of Duiliini.

Coframalaxius confirms this very special character as a probable morphological synapomorphy of the tribes mentioned by Emeljanov (2002). The structure of the prolegs was compared to the fossorial prolegs of cicada nymphs. We think the term "fossorial" is not appropriate, but the term raptor which Myers (1929) also mentioned is even less so. Based on the morphology of the proleg we suggest that it is more likely a double-grasping system (1) between the coxal apophysis and the femur, and (2) between the femoral apophysis and the tibia. This double-grasping mode would allow the nymph to firmly grab the roots and rootlets on which it feeds or use it to progress in the soil.

Forewing venation

In the Fulgoromorpha ground pattern (Shcherbakov, 1996; Bourgoin et al. 2015) the media vein of the tegmina forks once at the nodal line into and anterior branch and a posterior branch, both respectively forking again into MP_1, MP_2, and $MP_{3,}$ MP_4 (Fig. 9A) As mentioned by Emeljanov (2002), a five MP branchs probably belongs to the ground plan of the Cixiidae, but occurring in two different patterns. In most cixiids, the trifid anterior branch of the media (M_{1+2}) is realized by the first forking in MP_1 and MP_2 generally occurring between the nodal line and the submarginal line and the second forking of MP_1 into MP_{1a} and MP_{1b} at or after the submarginal line (Fig. 9B). The fork of the posterior branch of the media (MP_{3+4}) into MP_3 and MP_4 is generally part of the submarginal line. From this basic cixiid schema, a clear distinctive one with still five MP terminals but with a bifid anterior media branch (MP_1, MP_2) and a trifid posterior one (MP_3 and MP_4 forking into MP4a and MP4b) is present in Brixiini Emeljanov, 2002, Brixidiini Emeljanov, 2002 and some Mnemosynini (Emeljanov 2002) (Fig. 9C). Oecleini have the anterior trifide type (Fig. 9D). Often, individual asymmetrical variations occur in specimens, but this general pattern is more typical. In several genera, this pattern is often modified with a single posterior MP_{3+4} branch. Such a conformation is found in the following species:

Oecleus mackaspringi Myrie et al., 2019 (Myrie et al. 2019: Fig. 4 with MP_{3+4} misidentified as M_{2+3} and CuA_1 and CuA_2 misidentified as MP_4 and CuA)

Myxia hernandezi Bahder & Bartlett, 2021 (Zumbado Echavarria et al. 2021: Fig. 3 with MP_{1a}, MP_{1b}, MP_2 and MP_{3+4} respectively misidentified with MP_1, MP_2, MP_3, MP_4)

Myxia belinda Bahder et al., 2019 (Bahder et al. 2019) and *M. baynardi* Barrantes Barrantes et al. 2021B) (Barrantes Barrantes et al. 2021a) with Fig. 6 in both papers with MP_{1a}, Mp_{1b}, MP_2, MP_{3+4}, CuA_1+CuA_2 and icu respectively misidentified with MP_1, MP_2, MP_3, MP_4, CuA_1 and CuA_2.

In other oecleinian taxa a normal pattern is observed in *Haplaxius dougwalshi* Bahder et al., 2020, (Bahder et al. 2020) and *H. pococo* Bahder & Bartlett, 2021 (Barrantes Barrantes et al. 2021b), in the genus *Bothriocera* Burmeister, 1835, the amber fossil *Bothriobaltia* Szwedo, 2002 (Szwedo, 2002), *Oecleus* Stål, 1862 (Ball and Klingenberg 1935) and *Borbonomyndus* Attié, Bourgoin & Bonfils, 2002 (Attié et al. 2002). In

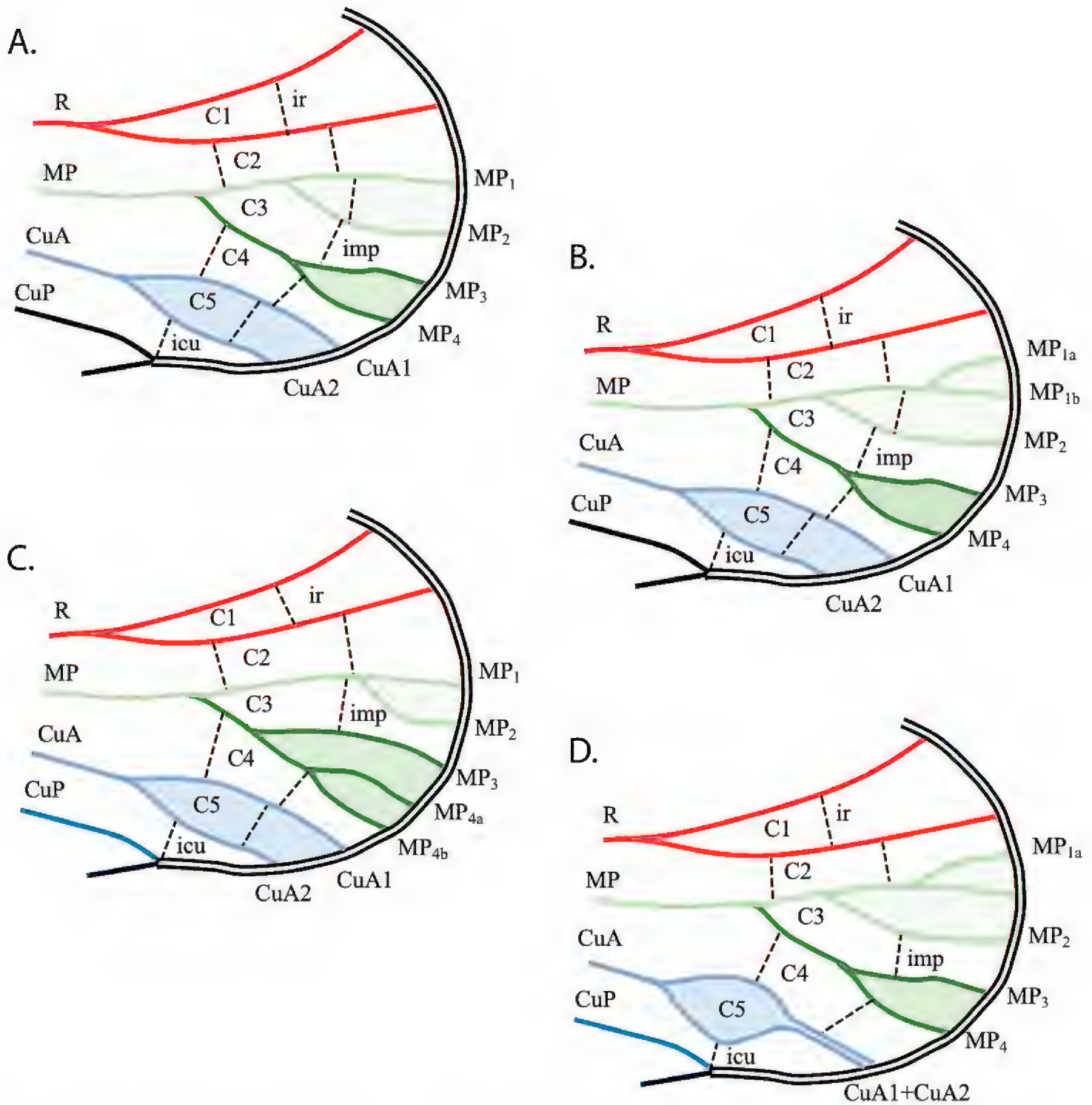

Figure 9. General patterns of MP and CuA veins in planthopper tegmina from (**A**) ground plan (according to Shcherbakov, 1996; Bourgoin et al. 2015), of the probable cixiid plesiomorphic condition (**B**), and with inverted patterns of anterior and posterior MP branches (**C**) in Mnemosynini and Pintaliini, and Oecleini patterns (**D**) with CuA branches fused (in many Oecleini MP3 and MP4 are also fused into a single MP_{3+4} terminal branch).

Meenocixius Attié, Bourgoin & Bonfils, 2002 (Attié et al. 2002) an unusual late forkings of MP_{1+2} and MP_{3+4} at the submarginal line in a 4-terminal MP is observed.

Most oecleine genera exhibit a short diamond shaped C5, distally closed in a single stem of CuA_1+$CuaA_2$ fused in a short stem after the nodal line, or totally fused in a single terminal (Fig. 9D). In *Borbonomyndus* (Attié et al. 2002) and *Bothriocera* (Emeljanov 2002), CuA_1 and CuA_2 remains separated with a probable plesiomorphic elongated C5. These various patterns may be of specific or even generic value, but don't seem stabilized at higher taxonomic rank.

Hindwing venation

Emeljanov (2002), addressed the anastomosis of MP+ CuA in the hind wings of Cixiidae. Four types of connections between the two veins can be described (Fig. 10). The probable most plesiomorphic type or U-type (Fig. 10) shows the two veins still connected by a short mp-cua transverse veinlet as in *Borysthenes* (Emeljanov 2002, fig.6b). The punctate anastomosis between MP_{3+4} and CuA_1 or V-type (Fig. 10) is found in *Andes* Stål, 1866 or *Pentastiridius* Kirschbaum, 1868, (Emeljanov 2002, fig. 5b, 6b), but a partial fusion of these two veins, or Y-type, seems to be more widely expressed in Cixiidae. The ultimate stage is the complete fusion of MP_{3+4} and CuA_1 (Fig. 10 I-type) found in several genera of various tribes: *Myndus* Stål, 1862, *Duilius* Stål, 1858, *Cajeta* Stål, 1866, *Pintalia* Stål, 1862, *Eucarpia* Walker, 1857, ... (Emeljanov 2002). While a trend to the fusion of MP_{3+4} with CuA_1 appears to be quite general in the family, it remains to be described in more genera to better appreciate if these different patterns carry further diagnostical or phylogenetical value. As in many other Oecleini, *Coframalaxius* belong to the I-type, together with the absence of forking of the anterior branch of the media.

Wax pore plates and associated sensory pits on abdominal termites VI–VIII in nymphs

Patterns of these tegumentary glands and sensory units were discussed by Emeljanov (1992), who later presented an evolutionary scenario of its transformation within the Cixiidae (Emeljanov 2002). He posited a five step morpholine with six types arising from a plesiomorphic type with the sensory pits anterior to the wax plates then becoming surrounded by the wax plates, then ultimately reduced to only one sensory pit surrounded by two smaller plates (Emeljanov 2002, fig.10). *Coframalaxius* is a good example of the intermediate type hypothesized by Emeljanov (2002): five sensory pits placed in the anterior row. However, another scenario where the *Coframalaxius* type, quite similar to the pentastirine one, could represent the plesiomorphic condition. It evolved on one side to an apomorphic condition for higher Oecleini taxa with the sensory pits migrated anteriorly to the wax plates (anteromarginal row in *Haplaxius* Fowler, 1904) and on the other side to the multiplication of the lateral sensory pits (Pentastirini) or the progressive fusion of the lateral wax plates with reduction of the sensory pits in the cixiinian lineage. As mentioned by Emeljanov (2002) the absence of better knowledge of nymphs of most cixiid tribes is distressing.

Metatibial spines

Two minutes lateral tibial spines are typical of cixiid early nymphs as in *Coframalaxius* (Fig 6D). These spines were present in adult Cixiidae in various numbers, and their absence in adults is interpreted as apomorphic by Emeljanov (2000, 2002) according to his hind leg "disarmament evolutionary scenario". They are absent in adult oecleines

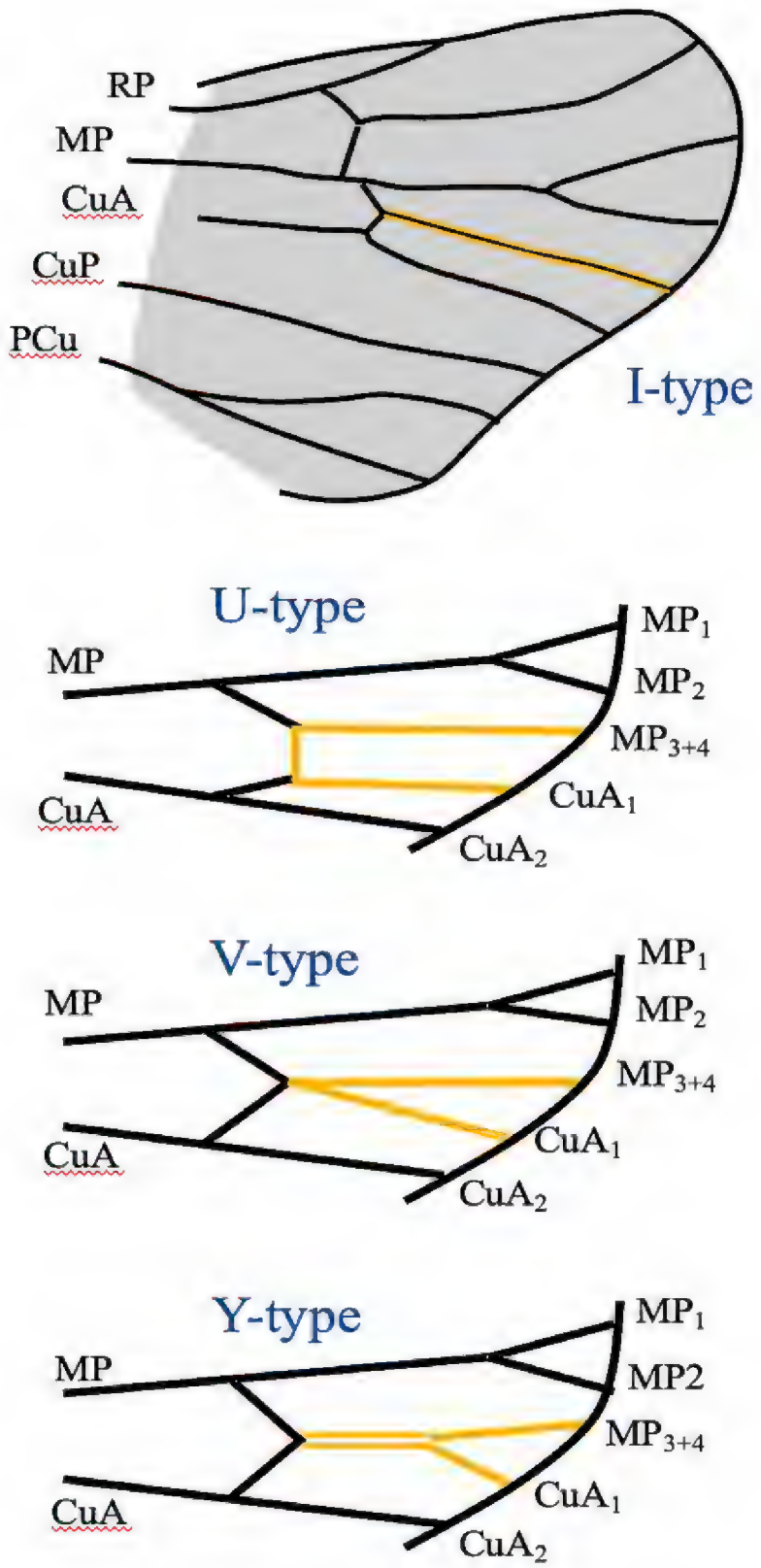

Figure 10. Types of connections between MP and CuA veins in planthopper hindwings. General conformation and respective U-, V-, Y- and I-type observed in Cixiidae.

with the exception in the cave genus *Confuga* Fennah, 1975, in which six minute lateral spines are found (Santos et al. 2019: fig. 8). This condition might be linked to the cave-living adaptation of this species by retention of a nymphal condition in the adult. Lateral spines are present in the other adult cixiids (Emeljanov 2002) - with a few exceptions such as their absence in *Pentastiridius* (*Podaplus*) Emeljanov, 1995, and together with presence of a diastema as in the Uzbekistan species *Pentastiridius* (*Podaplus*) *subterraneus* Emeljanov, 1995). The diastema seems characteristic of the oecleine lineage tribes (Emeljanov 2002).

3. Ecological classification

In the cave, specimens (adults and nymphs) were found in two different "cixiid nests" made of aggregated rootlets by abundant waxy filaments (Fig 1) and forming distinct galleries, in which the specimens were walking. These nests were located in the transitional but obscure zone of the cave at about 1 m from the cave floor for the first one. Several other smaller waxy nests were observed in other root masses, but no adults were observed there. All adults remained inside the nest and were never observed isolated outside the nest. When disturbed, adults would slowly walk away, and were never observed jumping or even flying. In several places in the deep cave zone, nymphs (at least 3rd to 5th instar) were observed walking on the rock surface of the cave walls, usually close to the floor and often close to small roots.

The cave is located in an area well studied with regard to its epigean fauna and which has been regularly sampled over many years, however no epigeal population had ever been reported. Like all cixiids, the nymphs live in a hypogeous environment, but the adults also stay underground - without being forced to do so by the ants who would exploit them for trophobiosis (Myers 1929; Bourgoin et al. in prep). The adults live together in the "cixidian nest" consisting of rootlets and waxy filaments produced by the nymphs of different stages which are present along the adults. In the nest, specimens can most likely communicate via the root substrate as do other planthoppers (Hoch and Howarth 1993; Soulier-Perkins et al. 2007), feed and reproduce there. Thus, Cofromalaxius remains only known from the hypogean habitat where it completes its full life cycle. Based on our observaions, rather than a subtroglophile species living temporally or cyclically in hypogean conditions such as its sister taxa *Trigonocranus emmeae* (Hoch et al. 2013), *Coframalaxius bletteryi* should be considered as an eutroglophile species (Sket 2008: 1560). Further field investigations on the life history of *C. bletteryi* will confirm its ecological status.

4. Conservation

Coframalaxius bletteryi, having been found in a single cave in southern France, shows an extreme degree of endemism. The species is specialized to live underground presumably feeding on roots of epigean plants, and according to field observations, has a presumed small population size. These criteria comply with the IUCN Red Data Book categories "vulnerable", or even "endangered" (IUCN 2019). This categorization, however, must be regarded preliminary. It is conceivable that the cave where the only known specimens have been found, is but a window to a much more extended superficial underground compartment, or MSS (*milieu souterranin superficiel*, as described by Juberthie et al. 1980), which is well developed in the mountainous regions of Europe (Juberthie 1995). According to Juberthie (1995: 20) the MSS, especially in the Mediterranean regions, at lower elevations forms a mosaic of habitats.

It is thus likely that *C. bletteryi* has a wider distribution in southern France. Nonetheless, there are potential threats to the species and to its environment. Increased

publicity of the occurrence of the new species may increase the number of visitors and put the population of *C. bletteryi* at risk, either through collecting or vandalism, such as damaging roots by trampling or voluntary destruction. Indirect, yet no less severe threats may come from threats to the surface environment, such as droughts, forest fires, as well as deforestation, road construction, and other alteration of surface vegetation. Extirpation of the population in the respective cave would perhaps not mean extinction of the species, however, it would destroy the unique chance to investigate the biology of one of France´s rarest endemic species.

Acknowledgements

We thank all the colleagues who allowed the field trip leading to the discovery of this new species to take place in these excellent conditions: CDS 06, Club Magnan with Alexandre Vandekerkhove and the Sofitaupes Club with Frédéric Bonacossa, Michel Radecki and Eric Madeleine for offering us their expertise on the cavities of the East-Var sector. A huge thank you to Jean-Michel Lemaire, for his particularly fruitful prospecting advice and for having been available day by day to guide us through the meanders of the valleys of the Alpes-maritmes. Special thanks to Emilie Gohier and Denwal Lecoq for their precious help during the field trip, to Jonathan Blettery who guided us during all our field trip, and allowed us to explore the caves in complete security, and to Sunbin Huang for the photographies "*in vivo*" he took (Fig. 1). We also thank Jerôme Constant from the Royal Institute of Natural Science of Brussels and Mike Wilson from the National Museum of Wales for their loan of specimen of *Trigonocranus emmeae* Fieber, 1876 allowing us to compare the two species, and Deqiang Ai and Manon Bucher for the sequencing in the *T. emmeae* and *C. bletteryi*.

References

Attié M, Bourgoin T, Bonfils J (2002) The Cixiidae (Hemiptera, Fulgoromorpha) from Mascarenes islands and Madagascar. Endemism and description of new taxa from Réunion with notes on their host plants. European Journal of Entomology 99: 543–555. https://doi.org/10.14411/eje.2002.071

Bahder BW, Barrantes Barrantes EA, Zumbado Echavarria MA, Mou DF, Helmick EE, Bartlett CR (2020) A new species of planthopper in the genus *Haplaxius* (Hemiptera: Auchenorrhyncha: Fulgoroidea: Cixiidae) on palms in Costa Rica and a new country record for *Haplaxius skarphion*. Zootaxa 4767(4): 543–552. https://doi.org/10.11646/zootaxa.4767.4.4

Bahder BW, Bartlett CR, Barrantes Barrantes EA, Zumbado Echavarria MA, Humphries AR, Helmick EE, Goss EM, Ascunce MS (2019) A new genus and species of cixiid planthopper (Hemiptera: Auchenorrhyncha: Fulgoroidea) from the Reserva Privada el Silencio de Los Angeles Cloud Forest in Costa Rica. Zootaxa 4701(1): 65–81. https://doi.org/10.11646/zootaxa.4701.1.5

Ball ED, Klingenberg P (1935) The genus *Oecleus* in the United States. Annals of the Entomological Society of America 28(2): 193–213. https://doi.org/10.1093/aesa/28.2.193

Barrantes Barrantes EA, Zumbado Echavarria MA, Bartlett CR, Helmick EE, Bahder BW (2021) A new species of planthopper in the genus *Haplaxius* (Hemiptera: Auchenorrhyncha: Fulgoroidea: Cixiidae) from coconut palm (*Cocos nucifera*) in Costa Rica. Zootaxa 4963(3): 412–422. https://doi.org/10.11646/zootaxa.4963.3.2

Bourgoin T (1988) A new interpretation of the homologies of the Hemiptera male genitalia, illustrated by the Tettigometridae (Hemiptera, Fulgoromorpha). In: Vidano C, Arzone A (Eds) Proccedings of the 6th Auchenorrhyncha Meeting, Turin, Italy, September 7–11, 1987. Consiglio Nazionale delle Ricerche-Special Project IPRA, Turin, 113–120.

Bourgoin T (1993) Female genitalia in Hemiptera Fulgoromorpha, morphological and phylogenetic data. Annales de la Société entomologique de France (N.S.) 29: 225–244.

Bourgoin T, Wang RR, Asche M, Hoch H, Soulier-Perkins A, Stroinski A, Yap S, Szwedo J (2015) From micropterism to hyperpterism: Recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). Zoomorphology 134: 63–77. https://doi.org/10.1007/s00435-014-0243-6

Bourgoin T (2022) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8, updated [2022-02-03]. http://hemiptera-databases.org/flow/

Burmeister HCC (1835) Schnabelkerfe. Rhynchota. Fascicule 1. In: Burmeister HCC (Ed.) Handbuch der Entomologie 2: 99–183

D'Urso V, Grasso R (2009) First record of troglobitic Fulgoromorpha from Italy (Hemiptera, Auchenorrhyncha, Cixiidae). Deutsche Entomologische Zeitschrift 56(1): 1–14. https://doi.org/10.1002/mmnd.200900002

Emeljanov AF (2002) Contribution to classification and phylogeny of the family Cixiidae (Hemiptera, Fulgoromorpha). Denisia 4: 103–112.

IUCN [International Union for the Conservation of Nature] (2019) IUCN Red List of Threatened Species. http://www.newworldencyclopedia.org/entry/IUCN_Red_List

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic biology 59(3): 307–321. https://doi.org/10.1093/sysbio/syq010

Hoch H, Howarth FG (1993) Evolutionary dynamics of behavioral divergence among populations of the Hawaiian cave-dwelling planthopper *Oliarus polyphemus* (Homoptera: Fulgoroidea: Cixiidae). Pacific Science 47: 303–318.

Hoch H (1994) Homoptera (Auchenorrhyncha Fulgoroidea). In: Juberthie C, Decu V (Eds) Encyclopedia Biospeologica. Société de Biospéologie, Moulis-Bucarest, 313–325.

Hoch H (2013) *Trirhacus helenae* sp.n., a new cave-dwelling planthopper from Croatia (Hemiptera: Fulgoromorpha: Cixiidae). Deutsche Entomologische Zeitschrift 60(2): 155–161.

Hoch H, Mühlethaler R, Wessel A (2013) Acoustic communication in the subtroglophile planthopper *Trigonocranus emmeae* Fieber, 1876 (Hemiptera: Fulgoromorpha: Cixiidae: Oecleini). Acta Musei Moraviae, Scientiae biologicae (Brno) 98(2): 155–162.

Hoch H, Sendra A, Montagud S, Teruel S, Lopes Ferreira R (2021) First record of a cavernicolous Kinnaridae from the Old World (Hemiptera, Auchenorrhyncha, Fulgoromorpha,

Kinnaridae, Adolendini) provides testimony of an ancient fauna. Subterranean Biology 37: 1–26. https://doi.org/10.3897/subtbiol.37.60483

Howarth FG, Moldovan OT (2018) The ecological classification of cave animals and their adaptations. In: Moldovan OT, Kovács L, Halse S (Eds) Cave Ecology, Ecological Studies 235. Springer Nature Switzerland, 41–67. https://doi.org/10.1007/978-3-319-98852-8_4

Juberthie C, Delay B, Bouillon M (1980) Extension du milieu souterrain en zone non-calcaire. Mémoires de Biospéologie 7: 19–52.

Juberthie C (1995) Underground habitats and their protection. Nature and Environment, No. 72. Council of Europe Press, 158 pp.

Lanfear R, Hua X, Warren DL (2016) Estimating the effective sample size of tree topologies from Bayesian phylogenetic analyses. Genome Biology and Evolution 8(8): 2319–2332. https://doi.org/10.1093/gbe/evw171

Letunic I, Bork P (2021) Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. Nucleic Acids Research 49 (W1): W293–W296. https://doi.org/10.1093/nar/gkab301

Luo Y, Bourgoin T, Szwedo J, Feng JN (2021) Acrotiarini trib. nov., in the Cixiidae (Insecta, Hemiptera, Fulgoromorpha) from mid-Cretaceous amber of northern Myanmar, with new insights in the classification of the family. Cretaceous Research 128: e104959. https://doi.org/10.1016/j.cretres.2021.104959

Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30(5): 1188–1195. https://doi.org/10.1093/molbev/mst024

Myers JG (1929) Observation on the biology of two remarkable cixiid planthoppers (Homoptera) from Cuba. Psyche 36: 283–292. https://doi.org/10.1155/1929/82326

Myrie W, Helmick EE, Bartlett CR, Bertaccini A, Bahder BW (2019) A new species of planthopper belonging to the genus *Oecleus* Stål, 1862 (Hemiptera: Fulgoroidea: Cixiidae) from coconut palm (*Cocos nucifera* L) in Jamaica. Zootaxa 4712(1): 127–137. https://doi.org/10.11646/zootaxa.4712.1.9

Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Racovitza EG (1907) Essai sur les problèmes biospéologiques. Archives de Zoologie Experimentale et Générale 4(6): 371–488

Sket B (2008) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42(21): 1549–1563. https://doi.org/10.1080/00222930801995762

Soulier-Perkins A, Sueur J, Hoch H (2007) Historical use of substrate-borne acoustic production within the Hemiptera: first record for an Australian Lophopid (Hemiptera, Lophopidae). Australian Journal of Entomology (2007) 46: 129–132. https://doi.org/10.1111/j.1440-6055.2007.00566.x

Szwedo J (2002) The first fossil Bothriocerinae from Eocene Baltic amber with notes on recent taxa (Hemiptera: Fulgoromorpha: Cixiidae). Deutsche entomologische Zeitschrift. Berlin 49(2): 197–207. https://doi.org/10.1002/mmnd.4810490204

Wilson SW, Tsai JH (1982) Descriptions of the immature stages of *Myndus crudus* (Homoptera: Fulgoroidea: Cixiidae). Journal of the New York Entomological Society 90: 166–175.

Wilson SW, Tsai JH, Thomson CR (1983) Descriptions of the nymphal instars of *Oecleus borealis* (Homoptera: Fulgoroidea: Cixiidae). Journal of the New York Entomological Society 91: 418–423.

Zhang D, Gao F, Jakovlić I, Zou H, Zhang J, Li WX, Wang GT (2020) PhyloSuite: an integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. Molecular ecology resources 20(1): 348–355. https://doi.org/10.1111/1755-0998.13096

Zumbado Echavarria MA, Barrantes Barrantes EA, Bartlett CR, Helmick EE, Bahder BW (2021a) A new species of planthopper in the genus *Myxia* (Hemiptera: Auchenorrhyncha: Cixiidae) from the Reserva Privada el Silencio de Los Angeles Cloud Forest in Costa Rica. Zootaxa 4915(3): 351–363. https://doi.org/10.11646/zootaxa.4915.3.4

Zumbado Echavarria MA, Barrantes Barrantes EA, Batlett CR, Helmick EE, Bahder BW (2021b) A new species of *Myxia* (Hemiptera: Auchenorrhyncha: Cixiidae) collected on palms from the Reserva Privada el Silencio de Los Angeles Cloud Forest in Costa Rica. Zootaxa 5027(3): 417–428. https://doi.org/10.11646/zootaxa.5027.3.7